BIOLOGY OF *SCOLIOPUS* (LILIACEAE) I. PHYTOGEOGRAPHY AND SYSTEMATICS[1]

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ABSTRACT

Comparisons of a wide variety of vegetative, floral, and reproductive characters of *Scoliopus* reveal consistent differences between the Californian *S. bigelovii* and the Oregonian *S. hallii*, whose distributions are mapped. With leaf numbers greater than two reported, a spiral, rather than opposite, leaf arrangement is demonstrated. The floral morphology and geometry, which involve intricate pollination subunits, are related to an outbreeding pollination system. A pollination subunit is established by the terminally recurved stylar arms, the versatile, extrorse anthers, the unusual triangular gynoecium, and the nectariferous, petaloid outer tepals. The myrmecochorous dispersal patterns in *Scoliopus* based on subterranean stems, elongate twisting pedicels, capsules dehiscing in the upper duff layers, and elaiosomal seeds are discussed. The taxonomic relationship to *Paris*, *Trillium*, and *Medeola* is deemed remote.

Scoliopus Torrey, a genus of two herbaceous perennials, occurs in the coastal montane regions of western North America, with the larger *S. bigelovii* Torrey restricted to California and *S. hallii* S. Watson to Oregon.

Detailed information on the distribution of *S. bigelovii* (Utech, 1979), floral vascular anatomy (Utech, 1979), pollination biology (Berg, 1959; Moldenke, 1976; Mesler et al., 1980), karyology (Johansen, 1932; Cave, 1966, 1970), seedlings (Rimbach, 1902), embryology, and dispersal (Berg, 1959, 1962b) has been published. However, beyond limited floristic accounts (Abrams, 1940; Peck, 1961; Hitchcock et al., 1969; Hitchcock & Cronquist, 1973), comparable data on *S. hallii* are lacking. Since 1979, *S. hallii* has been a watchlisted species among Oregon's rare, threatened, and endangered plants (Siddall et al., 1979; Eastman, 1990). Furthermore, *S. hallii* has been used by the federal Bureau of Land Management as a key indicator species for monitoring riparian plant communities in western Oregon.

Scoliopus is poorly represented in herbaria because it blooms very early in spring. With more populations now located and specimens of *S. hallii* available for study, as well as detailed field observations completed, a critical assessment of this interesting genus is now possible.

MATERIALS AND METHODS

Populations of *Scoliopus* from south of San Francisco, California, northward to Portland, Oregon, were marked and sampled. This study occurred during the early spring and summer of 1988 and 1990. Mass collections, where appropriate, were made for morphometric analysis throughout the ranges of *S. bigelovii* and *S. hallii*. Life history herbarium specimens of flowering and fruiting individuals from the same site were also made (Utech et al., 1984). Alcoholic collections, using FAA as the fixative, were made for anatomical (Johansen, 1940; Sass, 1958; Utech, 1979) and reproductive studies (Ohara & Kawano, 1986a, b; Kawano et al., 1986; Ohara & Utech, 1986, 1988; Ohara, 1989). Voucher specimens have been deposited at Carnegie Museum of Natural History (CM).

Fifty-six populations of *Scoliopus* were located: 35 for *S. bigelovii* and 21 for *S. hallii*. The *S. bigelovii* sites were in the following counties of California: Humboldt (9), Marin (4), Mendocino (7), San Mateo (4), and Sonoma (11). The *S. hallii* sites were in the following counties of Oregon: Benton (2), Clatsop (1), Douglas (2), Lane (4), Lincoln (1), Linn (5), Polk (3), and Tillamook (4). The exact locations of these study and/or collection sites are cited in the specimens examined section.
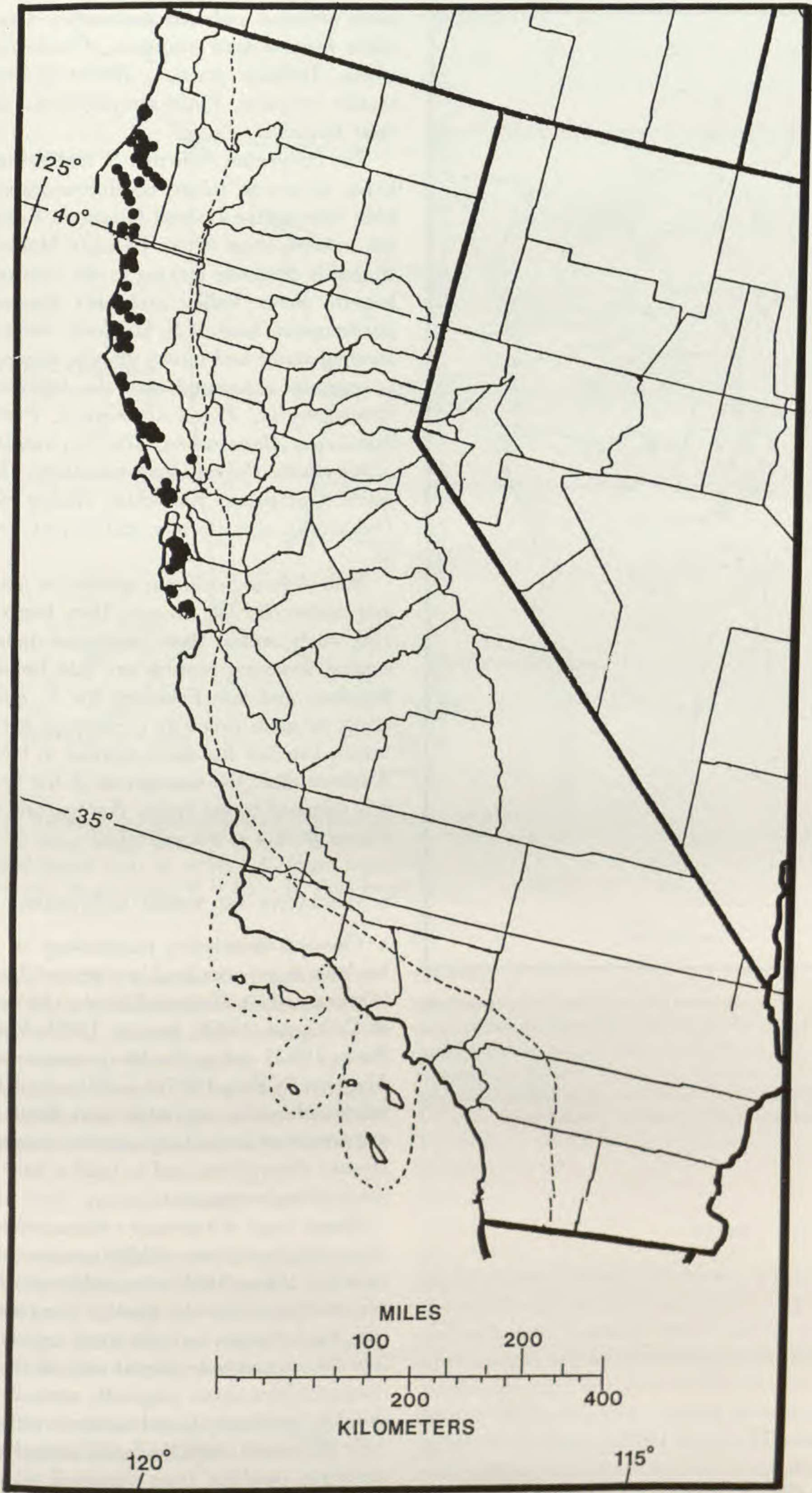
FIGURE 1. Distribution of *Scoliopus bigelovii* along the northwestern California coast. Crest of Coastal Mountain Range indicated by dashed line.
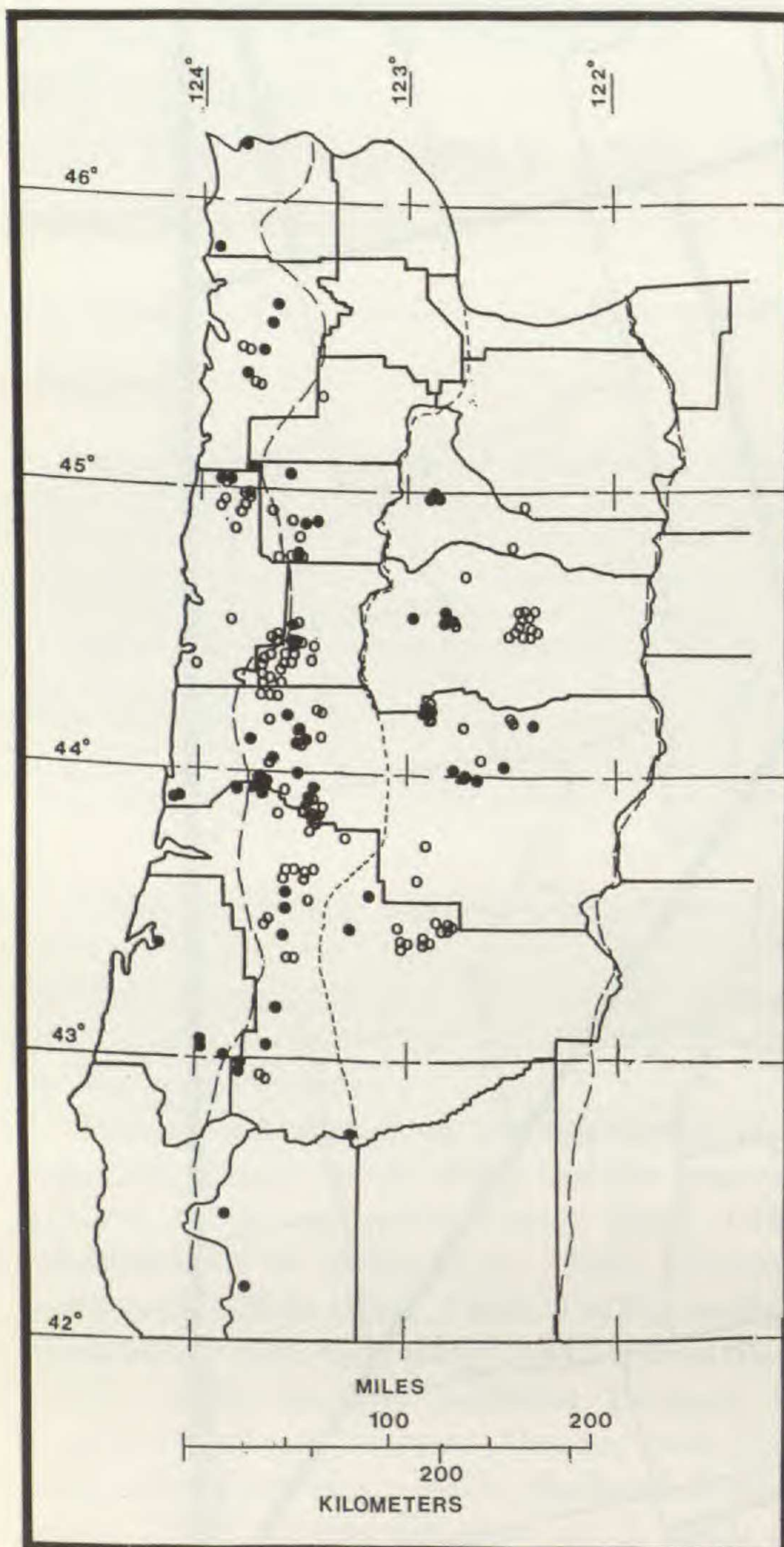
FIGURE 2. Distribution of *Scoliopus hallii* in western Oregon. Solid circles are herbarium-based locations, open circles are site records from the Bureau of Land Management (BLM) data base. Crests of Coastal and Cascade mountain ranges are indicated by long dashed lines, the Willamette River Valley by short dashed lines.

RESULTS

1. HABIT AND HABITAT

This small genus of two distinct species of perennial herbs occurs primarily in the old growth coniferous forests of far western North America. In the shady mesic understory slopes of the coastal Californian redwood forests (Stebbins & Major, 1965; Barbour & Major, 1977; Raven & Axelrod, 1978), from Humboldt County south to the Santa Cruz Mountains, *Scoliopus bigelovii* is relatively common (Fig. 1). According to my field observations and the ecological work of Smith (1957), its

more common redwood understory associates include *Polystichum munitum, Clintonia andrewsiana, Trillium ovatum, Dentaria integrifolia, Oxalis oregana, Viola sempervirens,* and *Trientalis latifolia.*

The Oregonian endemic, *S. hallii,* on the other hand, occurs in mixed coniferous habitats along both sides of the Coastal Mountain Range and on the western slope of the Cascade Mountains (Fig. 2), but is definitely lacking in the intervening Willamette River Valley and only approaches the northernmost limit of *S. bigelovii.* Never far from running water and mossy alluvial slopes, *S. hallii* is typically associated with the following: *Tsuga heterophylla, Picea sitchensis, Pseudotsuga menziesii, Alnus rubra, Acer circinatum, A. macrophyllum, Polystichum munitum, Oxalis oregana, Oplopanax horridum, Rubus spectabilis, Osmaronia cerasiformis,* and *Senecio triangularis.*

Both of these *Scoliopus* species are under studied and undercollected because they begin flowering very early within their respective habitats. The earliest flowering records are mid January for *S. bigelovii* and late February for *S. hallii.* Flowering, or more precisely continuous floral presentation, can last for three months in both species. A month after the emergence of the first flowers, it is common to see fruits, flowers, and even buds arising from a given individual.

2. VEGETATIVE AND FLORAL MORPHOLOGY

Classical descriptive morphology of *Scoliopus* has been largely confined to scattered floristic works (Abrams, 1940; Hitchcock et al., 1969; Hitchcock & Cronquist, 1973; Jepson, 1922; Munz, 1959; Peck, 1961) and to the biosystematic work on *S. bigelovii* by Berg (1959) and Utech (1979). Summaries of major vegetative and floral characters are presented here to support the comparative systematic descriptions and to build a base for future sister-group comparisons.

Roots and Rhizomes. Associated with the short, simple rhizomes of both species are extensive networks of long-lived, contractile roots. These roots are relatively long and thick in comparison to the thin, hard rhizome and effectively anchor the plants into the compacted, alluvial soils of their riparian habitats. New roots originate annually near the growing proximal tip and contract within the first year (Rimbach, 1902). Small annual growth increments resulting from cataphyll and leaf scars are identifiable along the rhizome. Because decay occurs distally, precise maximum aging is difficult.
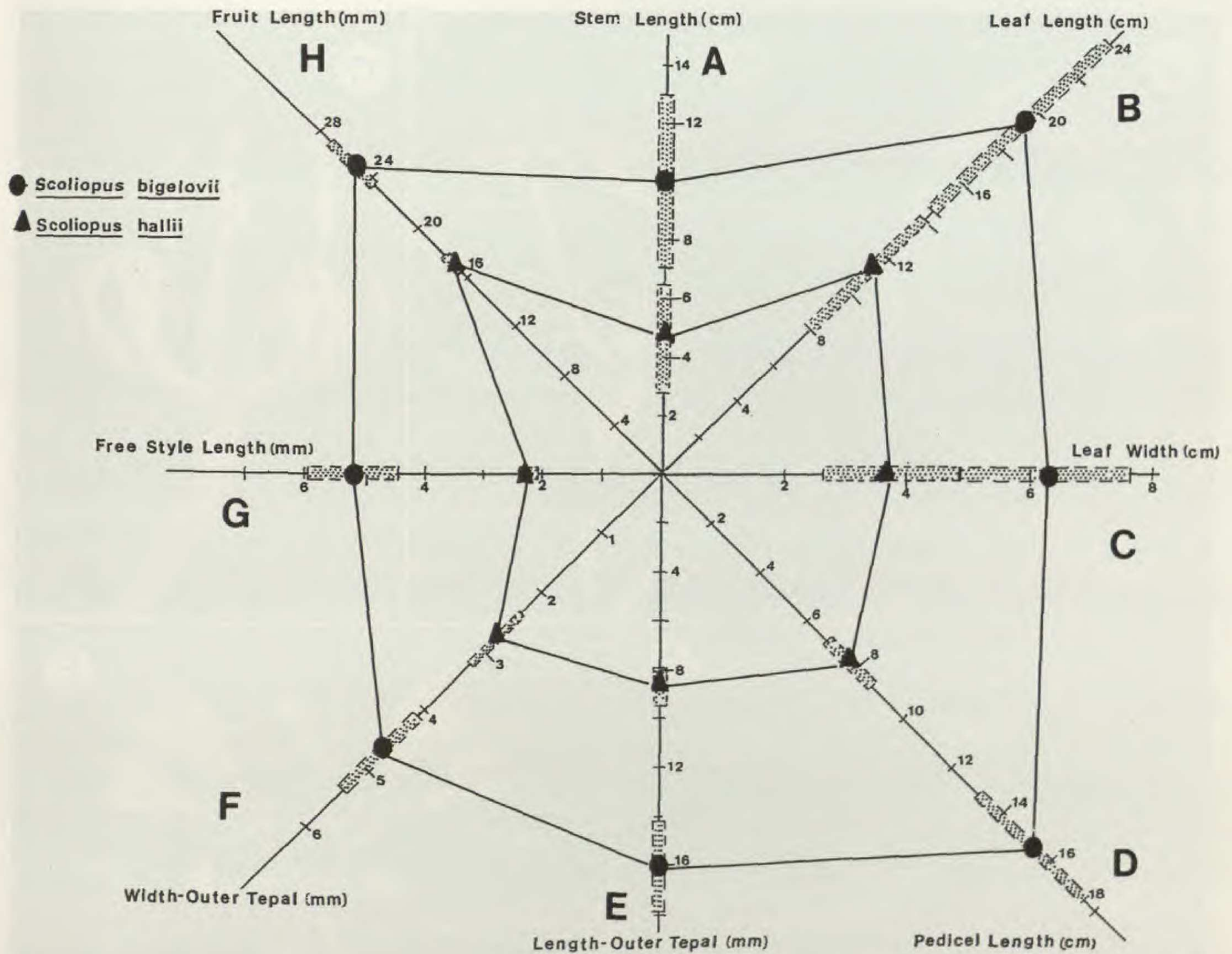
FIGURE 3. Variation polygon comparing morphological characters in *Scoliopus bigelovii* (circles) and *S. hallii* (triangles).—A. Stem length (cm), N = 50.—B. Leaf length (cm), N = 50.—C. Leaf width (cm), N = 50.—D. Fruiting pedicel length (cm), N = 50.—E. Outer tepal length (mm), N = 35.—F. Outer tepal width (mm), N = 35.—G. Free style length (mm), N = 35.—H. Fruit length (mm), N = 35. Shaded bars = standard deviation units.

However, ages of 20 years can be frequently established for mature individuals of both species.

Flowering and/or fruiting individuals of each species often occur so close together they appear to have a common rhizome. When such clumped individuals are dug and their root systems carefully washed, separate rhizomes and associated roots are evident.

Rarely in both species, rhizomes that had accidentally split or forked at the proximal growing tip were discovered. Subsequently, upon progressive decay of the rhizome's distal portion, two separate, vegetatively produced individuals result. These resulting plants have a common, genetic rootstock system, as demonstrated in *Smilacina* and *Polygonatum* (Kawano, 1975, 1985), and shoots that have an identical phenology. Other modes of vegetative reproduction were not observed in either species.

Stems. The unbranched stems in *Scoliopus* are short, vertical and, more importantly, subter-ranean, a significant adaptation to the high frequency of flooding in their environments. Each monopodial stem extends from its more or less horizontal rhizome to the upper duff layer.

Stem lengths generally coincide with rhizome depths. They vary from 5.5 to 20.5 cm (average 10.0 cm) in *S. bigelovii* and from 2.5 to 10.0 cm (average 4.6 cm) in *S. hallii* (Fig. 3). The average ratio of stem : cataphyll length was 1.76 in *S. bigelovii* (SD = 0.45) and a similar 1.75 in *S. hallii* (SD = 0.43). Slight increases in stem length occur in both species following anthesis.

An elongated, tawny brown stem sheathing cataphyll plus the remaining cataphyll fibers from previous years are found at the stem's base. At maturity, the current year's cataphyll lengths average 5.8 cm (3.5–8.5 cm) in *S. bigelovii* and 2.7 cm (1.5–5.0 cm) in *S. hallii*.

The whitish green, subterranean stems are fragile and not highly differentiated, being composed of large, thin-walled parenchyma cells with large

FIGURE 4.   Habit and floral geometry in *Scoliopus.*—A. Redwood understory habitat of *S. bigelovii* in flower.—
B. Enlarged view of *S. bigelovii* showing the relationship of tepals to stamens.—C. Enlarged side view of *S. hallii*
showing the spatial relationship of floral parts.—D. Mossy coniferous understory habitat of *S. hallii.*—E. Axial floral
view of *S. hallii* showing the recurved stylar arms and nectariferous glands on the outer tepals. (Photographs A, B
courtesy W. Knight; C–E, J. Erwin.)

intercellular spaces which surround the vascular
tissue. A subepidermal layer of collenchyma cells
that occurs in several longitudinal ridges does pro-
vide some mechanical support. With their stems
subterranean and totally out of view, both species
of *Scoliopus* are thus functionally acaulescent, but
not so morphologically.

Leaves. The emerging leaves are very short
as the earliest buds reach anthesis. Leaf enlarge-
ment, and particularly elongation, occur during,
and especially after, the flowering of the last bud.
Lengths of 15–24 cm and widths of 5–8 cm are
typical in *S. bigelovii* and 11–14 cm by 3–5 cm
in *S. hallii* (Figs. 3, 4; Hooker, 1897). Though
there is greater leaf variation in *S. bigelovii*, the
length : width (L : W) ratios for the two species
show nearly identical proportions (Table 1).

The elliptic to oblong leaves have obtuse to apic-
ulate tips and basally sheath and subterranean stem.

The dark green upper leaf surfaces of *S. bigelovii,*
which are paler below, are mottled with brownish
purple spots (Fig. 4A), while those of *S. hallii* are
frequently not mottled (Fig. 4D). The mature leaves
of *S. hallii* are more petiolate than the elongate,
clasping ones in *S. bigelovii.* Stomata occur only
on the lower, and paler, leaf surfaces of both spe-
cies.

Leaf venation in *Scoliopus* is parallel. The major
and parallel veins are interconnected with numer-
ous, nearly transverse minor veins. The resulting
venation pattern is definitely not reticulate. In *S.
bigelovii*, there are seven to nine of these large,
longitudinal veins. Of these, five are sunken into
the laminal surface. The lower leaf surfaces are
thus ribbed or keeled by these veins. Only three
such sunken veins occur in *S. hallii.* In both spe-
cies, these major sunken veins fuse at the leaf
apex, while the other parallel veins simply end.

TABLE 1. Comparative *Scoliopus* morphometrics.

Character	Taxa	
	S. bigelovii	*S. hallii*
Leaf		
Length (cm)	19.20 ± 4.67* (14.5–23.9)* N = 50*	11.04 ± 3.04 (8.0–14.1) N = 50
Width (cm)	6.27 ± 1.42 (4.8–7.7) N = 50	3.73 ± 1.11 (2.6–4.8) N = 50
L:W ratio	2.98 ± 0.92 (2.0–7.1) N = 50	3.00 ± 0.47 (2.1–4.0) N = 50
Pedicel length (cm) (flowering)	15.32 ± 2.20 (11.0–22.0) N = 50	7.73 ± 0.95 (6.0–9.8) N = 50
Flower number / plant (herbarium and field)	4.49 ± 2.32 (1–15) N = 400	2.06 ± 1.04 (1–5) N = 287
Outer tepal		
Length (mm)	16.15 ± 1.94 (12.6–19.3) N = 50	8.69 ± 0.76 (6.8–10.0) N = 50
Width (mm)	4.75 ± 0.65 (3.0–6.0) N = 50	2.79 ± 0.42 (2.0–3.3) N = 50
L:W ratio	3.44 ± 0.52 (2.6–5.1) N = 50	3.19 ± 0.55 (2.1–4.4) N = 50
Inner tepal		
Length (mm)	15.47 ± 1.85 (11.6–19.0) N = 50	7.48 ± 0.71 (6.0–9.0) N = 50
Width (mm)	0.54 ± 0.09 (0.3–0.7) N = 50	0.35 ± 0.10 (0.2–0.8) N = 50
L:W ratio	29.32 ± 6.05 (16.6–46.7) N = 50	22.56 ± 5.02 (10.0–37.5) N = 50
Filament length (mm)	3.76 ± 0.41 (2.3–4.3) N = 50	3.13 ± 0.39 (2.0–3.7) N = 50
Anther length (mm)	2.39 ± 0.22 (2.0–2.8) N = 50	2.17 ± 0.15 (1.9–2.3) N = 50
Free stylar arm length (mm)	5.26 ± 0.81 (4.5–6.1) N = 50	2.26 ± 0.18 (2.1–2.4) N = 50
Fruit		
Length (mm)	25.17 ± 1.93 (22.5–29.5) N = 50	17.21 ± 0.66 (16.0–18.5) N = 25

TABLE 1. Continued.

Character	Taxa	
	S. bigelovii	*S. hallii*
Width (mm)	7.66 ± 0.58 (6.3–9.0) N = 50	6.63 ± 0.66 (5.5–7.5) N = 25
L:W ratio	3.31 ± 0.36 (2.8–4.0) N = 50	2.62 ± 0.28 (2.1–3.4) N = 25

* Mean ± s.d., range of values, sample size.

Leaf arrangement in *Scoliopus* is spiral and not, as often stated, paired or opposite. Such terminology implies a derived two-leaved whorl or opposite state and thus a relationship to the multi-leaved whorls of other Paridean genera with reticulate venation, e.g., *Paris* or *Trillium*.

Individuals of *S. bigelovii*, with four leaves, and *S. hallii*, with three, have been observed and collected from throughout their respective ranges. Population samples establishing the frequency of leaf numbers for both species are presented in Table 2. The three-leaved condition is relatively common in mature individuals and stable populations of *S. bigelovii*. Though Berg (1959) encountered plants with only two leaves in his study of *S. bigelovii*, historical accounts note three-leaved (Eastwood, 1932) and four-leaved (Brandegee, 1891) plants. In plants of either species with more than two leaves, the sheathing leaves have an observable, spiral arrangement at their insertion on the subterranean stem, though their internodes are greatly reduced.

Inflorescence. Examination of a stem's subterranean crown, from which the numerous pedicels appear to arise, reveals several fascicles of pedicels. Each axillary fascicle, up to three in *S. bigelovii* and two in *S. hallii*, is composed of 2–5 pedicels separated by short internodes. The flowers of the upper fascicles bloom later than those of the lower. A leaf is associated with each fascicle. Bracts are lacking throughout the inflorescence. Plants with more leaves tend to have more flowers. Berg's (1959) morphological analysis of the crown showed that a fascicle might be either a contracted bostryx or a contracted cincinnus. Another possibility, which I envisioned, is a contracted raceme.

The maximum number of flowers per plant is best determined by counting pedicels at the end of flowering, since the order of flowering is irregular and prolonged. A frequency distribution comparing the number of flowers (i.e., pedicels) for both spe-
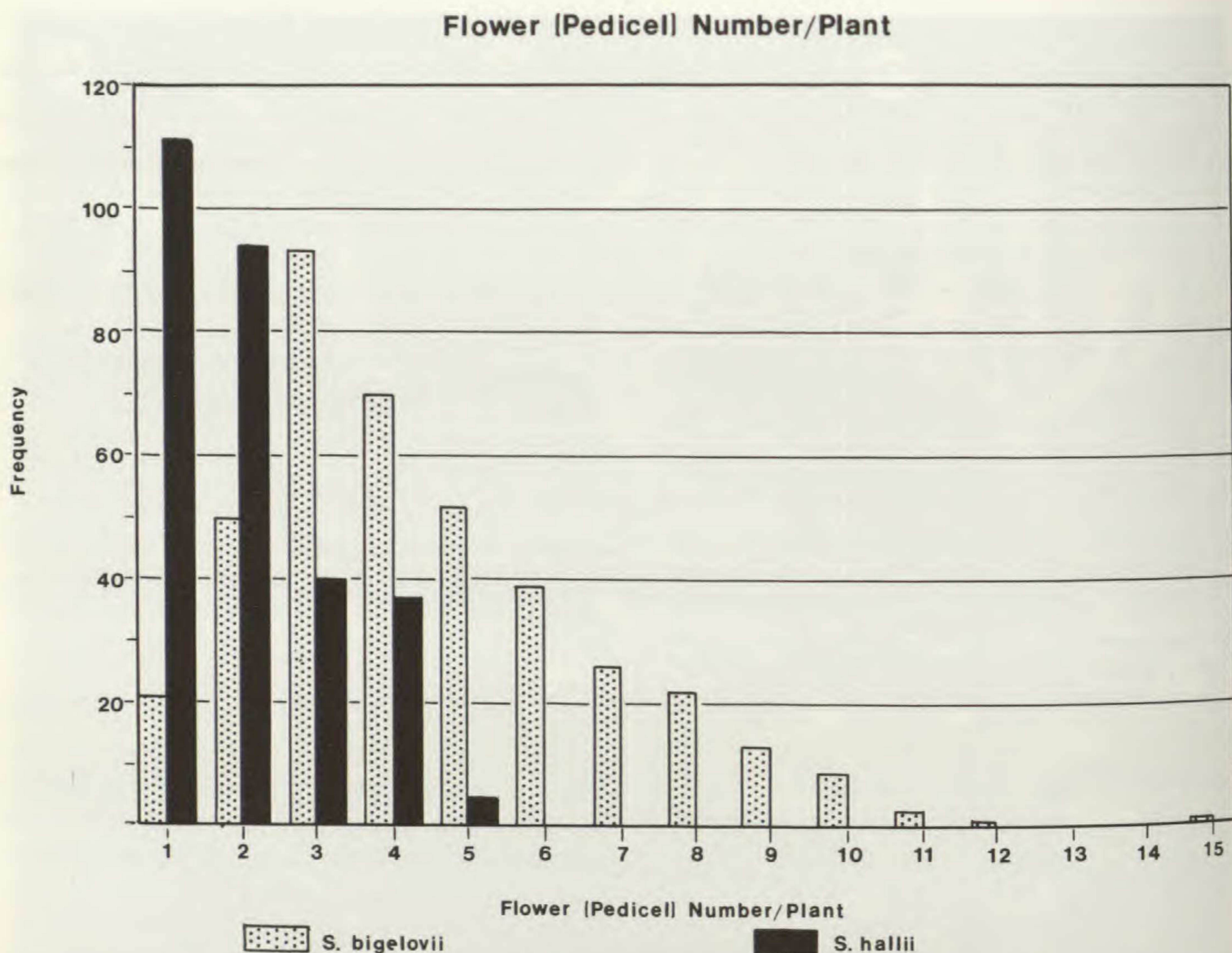
Flower (Pedicel) Number/Plant

FIGURE 5. Frequency distribution showing the number of flowers (or pedicels) per plant in *S. bigelovii* (shaded bars) and *S. hallii* (solid bars).

cies is presented in Figure 5. A greater range occurs in *S. bigelovii* (1–15) than in *S. hallii* (1–5), though their averages are less dissimilar: *S. bigelovii* (4.5) versus *S. hallii* (2.1) (Table 1).

Floral Morphology and Anatomy. The showy, ill-scented flowers of *Scoliopus* are tetra-cyclic and thus deviate from the typical liliaceous arrangement in lacking three inner stamens.

The flowers of *S. bigelovii* are significantly larger than those of *S. hallii*, though both exhibit a similar proportion in their floral geometry. While the lengths and widths of the large, petaloid outer tepals of *S. bigelovii* are nearly twice as large as those of *S. hallii* (Figs. 3, 4), their respective length : width ratios are nearly identical. The lengths of the narrowly erect inner tepals of *S. bigelovii* are nearly twice as large as those of *S. hallii*, though their widths differ only slightly (Table 1).

The three outer stamens opposite the outer tepals are basally adnate to these tepals for 0.5 mm in *S. bigelovii* and 0.2 mm in *S. hallii*. The free filaments are short (averaging 3.7 mm in *S. bigelovii* and 3.1 mm in *S. hallii*; Table 1), slightly

dilated in transverse section, and curved outwards at the level of anther attachment (Fig. 4B, C, E).

The greenish yellow, oblong anthers are adaxially attached near their mid-lengths. The connective tissues between the anther sacs are flat, though the sacs are free, versatile, and divergent basally. The endothecial cells lining the anther sacs have banded thickenings. Extrorse dehiscence is via two vertical abaxial slits. The tepals and anthers are not persistent.

Unlike most tricarpellate, syncarpous, liliaceous gynoecia in which the dorsal regions correspond to the corners or ribbed portions of the pistil, the dorsal regions in *Scoliopus* are laterally flattened or compressed, and the ventral regions occupy the corners of the triangular pistil. The strongly triangular gynoecium is formed by limited fusion along the ventral/septal margins, which subsequently form the corners (Fig. 6). Raphides were not observed in floral tissue of either species.

Most liliaceous gynoecia with laterally fused septal wings that protrude extensively into the common locular space have some type of axial placentation
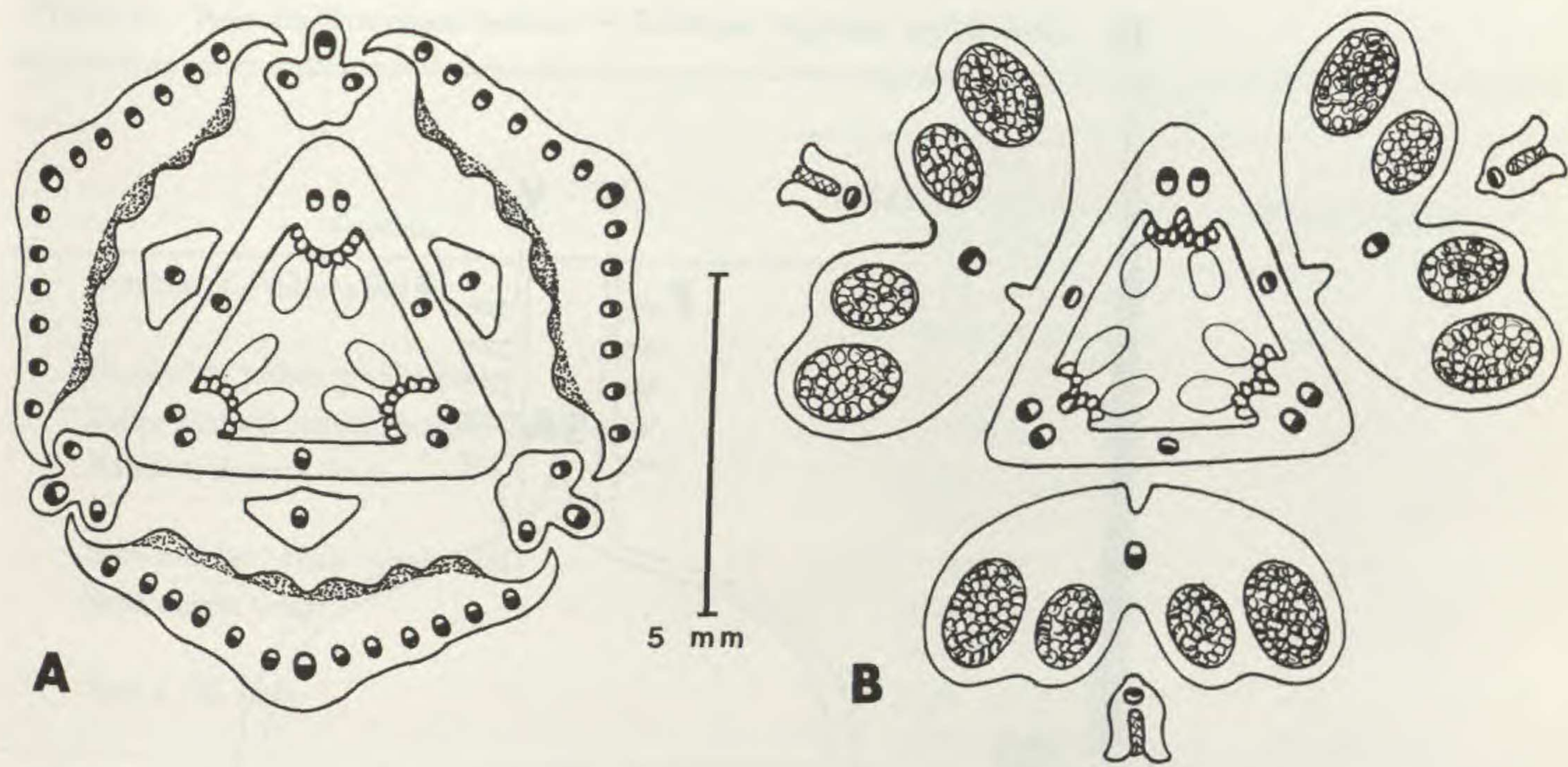
FIGURE 6. Transverse sections showing floral morphology and geometry in *Scoliopus bigelovii.*—A. Section through lower floral envelope and triangular gynoecium showing the large, petaloid outer tepals with numerous veins and nectariferous surfaces (shaded), three outer stamens (inner stamen lacking) opposite the flush dorsal surfaces, and the unilocular gynoecium with three sets of two ranked ovules.—B. Section through middle floral envelope and gynoecium showing the position of the three recurved stylar arms with reversed conducting elements and the extrorse anthers of a pollination subunit. (Adapted from Utech, 1979.)

and three locules. Septal glands often occur between these lateral wings when septal fusion is incomplete.

In *Scoliopus*, the broadly unilocular gynoecium is highly unusual (Berg, 1959; Utech, 1979). Placentation is parietal, since the ventral bundles are in the corners and protruding septal wings are lacking (Fig. 6). Basally, the locules open initially outwards from the center along the dorsal radii, a hint of loculicidal dehiscence.

The shared ascending styles are short and subdivided along the dorsal radii into three, recurved stylar arms or branches. The stylar arms are longer in *S. bigelovii* (5.3 mm) than in *S. hallii* (2.3 mm) (Table 1). Terminally localized on the upper and inner surface of each arm are minute stigmatic zones (Figs. 4B, C, E, 8B), an obvious adaptation for outbreeding. Stigmatoidal tissue is continuous from the three recurved stigma tips down through the shared style and along the inner funicular-ventral margins.

The anatropous, bitegmic ovules are loosely arranged in two ascending rows in each of the three ventral corners (Fig. 6). The number of ovules per

TABLE 2. Leaf number variation in populations of *Scoliopus*.

| Species and populations	Number of leaves and percentage of population						Total number of plants
	2	%	3	%	4	%	
S. bigelovii							
Kings Mt.	16	64.0%	8	32.0%	1	4.0%	25
Camp Meeker	20	80.0%	5	20.0%	0	0.0%	25
Kneeland	20	80.0%	5	20.0%	0	0.0%	25
Herbarium	267	82.9%	55	17.1%	0	0.0%	322
Total	323	81.4%	73	18.4%	1	0.3%	397
S. hallii							
Siuslaw Creek	99	99.0%	1	1.0%	0	0.0%	100
McDowell Creek	100	100.0%	0	0.0%	0	0.0%	100
Herbarium	86	98.9%	1	1.1%	0	0.0%	87
Total	285	99.3%	2	0.7%	0	0.0%	287
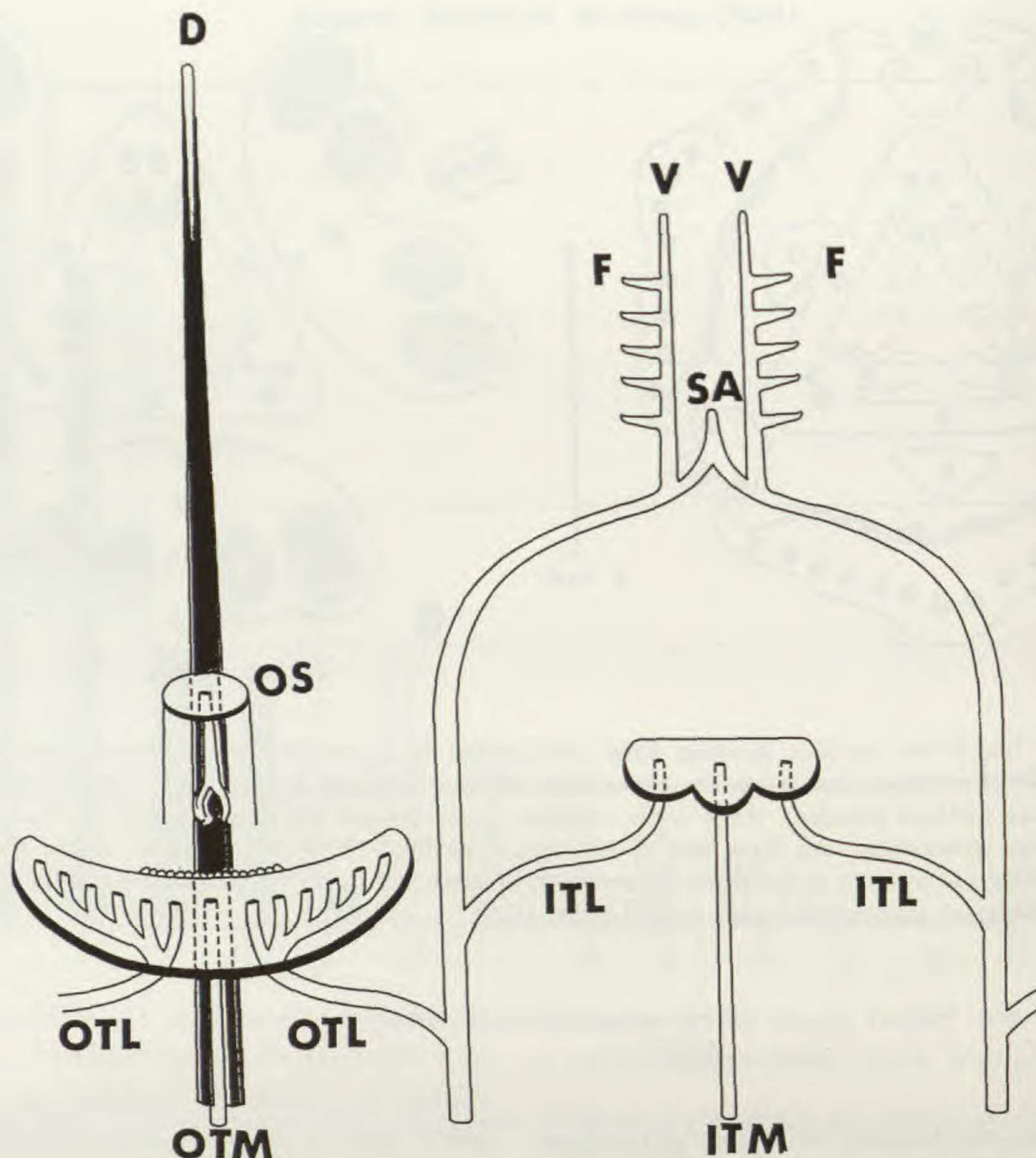
FIGURE 7. Summary longitudinal diagram showing the floral vascularization in *Scoliopus*. One-third of the floral network is presented. The basal portion of the bundle from which a dorsal (D) and an outer stamen (OS) are derived is not connected with an outer tepal medium (OTM) within the flower. There is no interconnection within the gynoecium of the dorsal and ventral supplies. The dorsals (D) are recurved outwardly into the stylar arms. Bundle codes: OTM = outer tepal median, OTL = outer tepal lateral, ITM = inner tepal median, ITL = inner tepal lateral, OS = outer stamen, D = dorsal, V = ventral, SA = septal axial, and F = funicular. (Adapted from Utech, 1979.)

pistil varies between 21 and 38 in *S. bigelovii* and between 20 and 32 in *S. hallii*, though their averages are nearly identical (Table 3). Embryo sac formation is of the *Polygonum* type, and endosperm formation is nuclear and unlike that in *Paris* and *Trillium* (Berg, 1959, 1962b).

The oblong to lanceolate, mature fruits are strongly three-angled and terminated by the persistent style. The mature fruits are generally larger in *S. bigelovii* than *S. hallii* (Table 1). The number of mature seeds per fruit is higher in *S. bigelovii* (Table 3). This is correlated to fruit size, since the seeds of both species are approximately the same size (Table 3).

The thin, membranous pericarp tissue dehisces or decays irregularly between the dorsals and ven-

trals. A maximum of six such zones occur per fruit (Fig. 6). One or two openings per fruit can expose all the seeds, since the capsules are unilocular. This irregular splitting or degeneration of parenchyma tissue does not follow the normal zones of weakness along the dorsal (loculicidal dehiscence) or the ventral (septicidal dehiscence) lines.

The *Scoliopus* fruit should be considered a capsule for the following reasons: it dehisces; it remains attached to the pedicel; and it possesses no pulpy tissue. Berg (1959) used the term "untypically loculicidal" for this type of capsule dehiscence and added further that "in comparison with other liliaceous capsules, the *Scoliopus* capsule must be considered highly reduced, because of its lack of sclerenchyma and normal dehiscence."

TABLE 3. Reproductive characteristics in *Scoliopus bigelovii* and *S. hallii*.

Criteria	Taxa	
	S. bigelovii California. Sonoma Co.: Camp Meeker	*S. hallii* Oregon. Linn Co.: McDowell Creek
Number of ovules/pistil	27.35 ± 3.77* (21.0–38.0)*	27.27 ± 3.07 (20.0–32.0)
Number of pollen grains/flower	2.10×10^4	1.65×10^4
Pollen number : ovule number (P : O) ratio	750 : 1	600 : 1
Number of seeds/fruit	14.28 ± 3.14 (10.0–22.0)	11.40 ± 1.20 (10.0–14.0)
Seed number/ovule number (%)	52.5%	41.8%
Seed weight (mg)	4.47 ± 0.31 (3.86–5.00)	3.15 ± 0.03 (3.10–3.20)
Seed L : W ratio	2.10 ± 0.15 (1.86–2.45)	2.05 ± 0.12 (1.86–2.25)

* Mean ± s.d., range of values.

3. FLORAL VASCULATURE

The floral vascularization of both *Scoliopus* species is similar to that presented in detail for *S. bigelovii* (Utech, 1979; Fig. 7). The floral vasculature is established from a 15-bundled, axial pedicel configuration, which consists of an outer zone of 12 bundles and an inner one of three large bundles. Six of the outer zone bundles depart directly as three outer tepal medians (OTM) and three inner tepal medians (ITM).

Each of the six remaining outer zone bundles undergoes two successive radial divisions whereupon 12 tepal laterals (6 OTL and 6 ITL) and six ventrals (V) are formed. Basally each of the six tepals receives three bundles, i.e., a median and two laterals, though the outer and inner tepals are quite dissimilar morphologically. Several radial divisions occur laminally among the outer tepal laterals (OTL) in *S. bigelovii* to create a maximum of 13 bundles, i.e., 12 laterals (OTL) and a median (OTM). No such subsequent radial divisions occur among the inner tepal laterals (ITL; Fig. 6A). The outer tepals of *S. hallii*, on the other hand, typically have a maximum of nine bundles, i.e., eight laterals (OTL) and a median (OTM).

Between each of the three pairs of ventrals (V) a fusion septal axial (SA) of short vertical duration is formed. Two-ranked, horizontal funicular traces (F) depart directly from each of the paired ventrals (V).

While the ventral vasculature has an outer zone origin, the three dorsal bundles (D) and the three outer stamen bundles (OS) are division products of

the three large inner zone bundles. No vestigial traces for inner stamen bundles nor for staminodes were observed in the material examined for this study of either species. The dorsals (D) are unbranched and terminate in the tips of the three recurved stylar arms. The dorsal (D) and ventral (V) supplies are not interconnected within the gynoecium.

4. FLORAL BIOLOGY

Many aspects of *Scoliopus* floral morphology are highly derived, advanced, or reduced and relate to specialized pollination (fungal gnats) and seed dispersal (myrmecochory). The structural geometry and adaptive significance of these showy, ill-scented flowers correlate with their mode of pollination. Berg (1959) correctly demonstrated for *S. bigelovii* (which also applies to *S. hallii*) that a single *Scoliopus* flower functions as three independent flowers, or pollination subunits, a feature usually associated with *Iris* (Figs. 4B, C, E, 7). This unusual partitioning of floral parts into subunits is described below.

Each of the three petaloid outer tepals is lined adaxially with nectariferous tissue. A broad floral cup or shallow tube is formed via the interpenetrating of the lateral edges of the outer tepals into grooves on the narrow, abaxial surface of the inner tepals (Fig. 6A). Because the triangular gynoecium is ridged along three outer ventral surfaces, which are opposite the narrow, appressed inner tepals and flattened along three dorsal surfaces (Fig. 6A), which are opposite the outwardly expanded outer

tepals and extrorse anthers (Fig. 6B), a configu-
ration of three independent pollination subunits is
established.

The three versatile, extrorse anthers dehisce
along two vertical abaxial slits (Fig. 6B). Pollen
dispersal zones are therefore defined between the
flattened dorsal regions of the gynoecium and the
expanded nectariferous grooves on the outer tepals.
Each of the three stylar arms recurves over the
top of an anther and exhibits a reversal in the
xylem to phloem arrangement (Fig. 6B). However,
the minute stigmatic surfaces are located terminally
and thus are removed from the pollen dispersal
zone.

The recurved styles, extrorse anthers, unusual
triangular gynoecium, and large, nectariferous out-
er tepals form a pollination subunit and are all
interrelated for outbreeding. The pollen : ovule (P :
O) ratios of 750 : 1 for *S. bigelovii* and 600 : 1
for *S. hallii* (Table 3), further assert limited out-
breeding.

Scoliopus bigelovii has been shown to be self-
incompatible (Berg, 1959; Mesler et al., 1980).
Fungal gnats in the closely related families My-
cetophilidae (*Mycetophila* sp.) and Sciarideae
(*Sciara* sp., *Corynoptera* sp.) were regarded as
pollinators, not merely nectar thieves, because of
high seed set and because they contacted anthers
and stigmas while feeding. Individuals captured on
the flowers carried pollen grains (Mesler et al.,
1980). The author has also observed fungal gnats
working the flowers of *S. hallii*.

Mesler et al. (1980) believed the high fruit and
seed set in *S. bigelovii* to be due primarily to the
abundance of fungal gnats and the corresponding
large number of flower visits. They thought the
frequency of pollination per individual gnat was
probably very low, but this was compensated for
by the large number of swarming gnats.

In the cool, moist redwood forests, where floral
resources are widely scattered, large, efficient but
energetically expensive pollinators, such as bumble
bees, are uncommon (Moldenke, 1976). Under
such habitat conditions, many plants could be ex-
pected to rely on small, relatively inefficient, but
presumably energetically cheaper vectors (Steb-
bins, 1974). Small dipterans, such as fungal gnats,
would be effective pollinators, both in terms of
overall fruit set and outcrossing potential, at least
when such insects are present in large numbers.
Seed setting percentages, based on the number of
seeds produced per ovule from the same sampled
population, were 52.2% in *S. bigelovii* and 41.8%
in *S. hallii* (Table 3).

5. SEEDS AND SEED DISPERSAL

The elongated fruiting pedicels that twist and
recurve to the ground have capsules that usually
open within the loose, moist coniferous duff. Pedicel
twisting is more pronounced in *S. bigelovii*. By
default, those seeds twisted en masse to the ground
would be group dispersed. Similar results would
also occur if ants progressively moved seeds to
their duff-hidden, midden heaps. The high density
of observed seedlings and adults in both species is
no doubt due to this means of dispersal.

Berg (1959) ably demonstrated that the seeds
of *S. bigelovii* were ant dispersed (*Formica fusca*
L., *F. fusca argentea* Whlr., *F. rufibarbis occidua*
Whlr., *Aphaenogaster subterranea occidentalis*
Em.) and documented the anatomy of the seeds'
oil-containing appendages or elaiosomes. Ant dis-
persal (*Formica* sp.) and seeds with similar elaio-
somes were observed in *S. hallii*.

Most myrmecochorous plants, like both species
of *Scoliopus*, begin flowering very early in spring
and continue producing seeds for some time
(Thompson, 1981). This phenological adaptiveness
insures a continuous supply of ripe seeds when the
ants are most abundant and active. The subter-
ranean stems, the fruiting pedicels twisting to the
ground, the capsules dehiscing in the upper duff
layer, and the elaiosome-appendaged seeds are in-
tegrated into an advanced dispersal pattern.

6. KARYOLOGY

Chromosome counts for both species of *Scolio-
pus* have been reported. Cave (1966) noted a count
of $2n = 14$ for *S. hallii*. However, Johansen's
(1932) report of $2n = 14$ for *S. bigelovii* was not
confirmed by Cave (1966, 1970), who observed
counts of $2n = 16$ from several different Califor-
nian populations. The karyotype consists of three
large and five small chromosome pairs. One pop-
ulation from Humboldt County, for example, had
a somatic number of $2n = 16$, but also had extra,
or small, meiotic chromosomes indicating a certain
proportion of structural hybridity within the north-
ern part of the range.

The chromosomes of *Scoliopus* are small in
comparison to those of *Trillium* (Cave, 1970), but
detailed karyotypes for both *Scoliopus* species need
to be established. The chromosomal base number
for *Trillium* and *Paris* is a similar $x = 5$ (Fedorov,
1969), while that for *Scoliopus* should be associ-
ated with both $x = 7$ and $x = 8$ until more critical
karyological research is done.

CONCLUDING REMARKS

Comparison of the ecological, anatomical, and morphological characteristics of the two *Scoliopus* species shows them to be quite distinct and demonstrates that *S. hallii* is more than a geographically isolated, minor-sized variant of *S. bigelovii* (Fig. 3; Table 1). Both have distinctive geographic distributions, ecological associations, and therefore different, past eco-evolutionary histories.

Two character suites epitomize the reduction and specialization within the genus—one for pollination, the other for ant dispersal. The floral morphology, anatomy, geometry, and phenology of both species attest to outbreeding and an unlikely, dipteran group of fungal gnats as present-day pollinators. The subterranean stems, elongate pedicels and duff dehiscing capsules over a prolonged time period support myrmecochory.

The large number of reduced or advanced characters in *Scoliopus* makes classification and analysis of these character assemblages difficult at times. Character clusters that deviate include tetracyclic flowers with nectariferous, petaloid outer tepals and no inner stamens, extrorse outer anthers, and modified unilocular gynoecia with parietal placentation.

Plants with more than two parallel-nerved leaves do occur in both species, and they are spirally arranged. The inflorescence should be viewed as one with axillary fascicles, not as an umbel.

The diagnostic characters that differentiate *Scoliopus* from *Paris* sensu lato, *Trillium*, and *Medeola* (the Englerian Parideae) have been clearly tabulated and documented (Berg, 1959, 1962a, b; Utech, 1978, 1979). *Scoliopus* is so different from these tribal cohorts that a brief historical and taxonomic review is warranted.

The traditional generic placement of *Scoliopus* in the Englerian Parideae with *Paris* (including *Kinugasa* and *Daiswa*), *Trillium*, and *Medeola* (Engler, 1888; Krause, 1930) or in the segregate family Trilliaceae (Hutchinson, 1934, 1959) has in recent years been questioned (Berg, 1959, 1962a, b; Utech, 1978, 1979; Takhtajan, 1983, 1986; Dahlgren et al., 1985).

Torrey (1857) described *Scoliopus* emphasizing the extrorse anthers and the axial placentation of the unilocular gynoecium and placed the genus tentatively at the end of the family Melanthaceae (Gray, 1856). Baker's view of Colchicaceae (1875, 1879) was similar to the above Melanthaceae, but included several "aberrant tribes," which did not fit. One was the monotypic Scoliopeae. In Watson's (1879) treatment of the North American Liliaceae,

a linkage among *Trillium, Medeola,* and *Scoliopus* was made. Recognizing the remote relationship between *Scoliopus* and the other two genera, *Scoliopus* was placed in its own subtribe Scoliopeae, apart from *Trillium* and *Medeola* in the tribe Trillieae.

Bentham & Hooker's (1883) acceptance of Watson's (1879) inclusion of *Scoliopus* in the Medeoleae (= Trillieae) was subsequently followed by Engler (1888), Krause (1930), Hutchinson (1934, 1959), and others. Hooker alone (1897) noted that *Scoliopus* was not closely allied to any of the group.

The aberrant and suspect tribal association of *Scoliopus* deserves revision. Few character sets of the tribe Parideae or the family Trilliaceae match those of *Scoliopus* or convey its proper taxonomic position. Following Watson, a tribal status coequal to *Trillium* and *Paris* would be one orthodox solution. Shifting *Scoliopus* as a monotypic tribe to the Uvulariaceae (Dahlgren et al., 1985; Takhtajan, 1986; Cronquist, 1988) would be another.

SYSTEMATIC TREATMENT

Scoliopus Torrey, Pacif. Rail. Rep. 4: 145, pl. 22. 1857. TYPE: *Scoliopus bigelovii* Torrey.

Glabrous, perennial herbs with short slender rhizomes; roots elongate, contractile. Stems short, unbranched, subterranean, not persistent. Leaves 2–3(–4), elliptic to broadly lanceolate, sessile-clasping to subsessile, apically obtuse to apiculate, parallel-veined with numerous transverse veins, dark green above, paler below, ± mottled with purple spots. Inflorescences contracted with several axillary fascicles of elongated, twisting pedicels. Flowers tetracyclic, showy, ill-scented. Perianth segments 6, in 2 series, dissimilar, distinct, deciduous; outer series 3, petaloid, many-nerved, striped, spreading, with basal nectariferous glands; inner series 3, erect, linear, 3-nerved, converging over the pistil. Stamens 3, opposite and adnate basally to outer segments; filaments free, hypogynous, filiform-subulate; anthers oblong, yellowish green, 2-celled, versatile, attached mid-length, extrorse, dehiscing via vertical abaxial slits. Ovary sessile, strongly 3-angled, unilocular, placentae 3-parietal, in locular angles; styles short, connate, erect; stylar arms 3, linear, horizontally spreading to recurved, channeled on the inner stigmatic surface; ovules 20–38, anatropous, bitegmic, in 2 rows on each placenta. Capsules brownish purple, beaked by persistent style and stylar arms, strongly 3-angled, thin-walled, opening irregularly, more by decay than dehiscence. Seeds 10–22, oblong, slightly

curved, sulcate-striate longitudinally, eliaosomes present. [Greek *skolios*, crooked, and *pous*, foot, allusion to the recurved, fruiting pedicels.]

KEY TO THE SPECIES OF *SCOLIOPUS*

1a. Leaves 14.0–24.0 cm long; outer petaloid segments 12.5–19.0 mm long; free stylar arms 4.5–6.0 mm long; coastal northwestern California .... 1. *S. bigelovii*
1b. Leaves 8.0–14.0 cm long; outer petaloid segments 6.5–10.0 mm long; free stylar arms 2.0–2.5 mm long; coastal mountains and western Cascade slopes of Oregon .... 2. *S. hallii*

1. **Scoliopus bigelovii** Torrey, Pacif. Rail. Rep. 4: 145, pl. 22. 1857 (fig. 8). SYNTYPES: U.S.A. California: Marin Co., Tamul Pass (Mt. Tamalpais), 1853, *Bigelow s.n.* (lectotype, NY, designated by Utech, 1979: 69; isolectotype, GH; photos CM). California: Sonoma Co., redwoods, Feb. 1856, *Samuels s.n.* (GH, NY, photos CM).

Stems subterranean, 6–20 cm long. Leaves 2(–4), elliptic to oblanceolate, sheathing at base, often mottled with purple, 14–24 cm long, 4.8–7.7 cm wide. Pedicels 3–12(–15), shorter than leaves at anthesis, greatly elongated, becoming strongly recurved to twisted in fruit, 11–22 cm long. Outer perianth segments ovate-lanceolate, mottled with green and lined with purple, up to 13-nerved, 12.5–19.0 mm long, 6.8–10.0 mm wide; inner segments linear-subulate, 11.5–19.0 mm long, 0.5 mm wide. Filaments 2.3–4.3 mm long, anthers 2.0–2.8 mm long. Capsules 22.5–29.5 mm long, 6.3–9.0 mm wide; stylar arms strongly recurved, 4.5–6.0 mm long; seeds 10–22. $2n = 16$.

Illustrations. Torrey (1857), Hooker (1897), Regel (1875), Abrams (1940), Parson (1907), Berg (1959), Utech (1979).

Representative specimens examined. CALIFORNIA: Coast Range, *Bolander s.n.* (MO), *Vasey s.n.* (GH, US). HUMBOLDT CO.: Hubbard's Station, *Davy & Blasdale 5399* (UC); T4N, R2E, S27, *Anderson 1938* (HSC); Bald Mt. Road, T6N, R2E, *Anderson 2397* (HSC); Indian Creek on Kneeland-Bridgeville Road, T2N, R4E, S6, *Anderson 2904* (HSC); Cow Creek fire-trail, headwaters Bear Creek, *Constance 836* (JEPS); Dinsmores, *Eastwood & Howell 4778* (CAS); Carlotta, *Hawver s.n.* (CAS); 200 ft., *Tracy 6144* (UC); 6 mi. S of Pepperwood, T1S, R2E, S14, 500 ft., *Johnson 108* (HSC); S Fork Bear Creek, 2.5 mi. S of Shelter Cove, 1,840 ft., *Kelly 301* (HSC); Kneeland Prairie, 2,000 ft., *Kildale 520* (DS); 2,500 ft., *Tracy 4060, 14808, 16862* (UC); Camp Bauwer Park, 0.25 mi. NE of Korbel, 190 ft., *Miller 1* (HSC); E of US 101 from Seawood Drive, T8N, R1E, S8, *Miller 128* (HSC); Eureka, *Paulson s.n.* (DS); 1.5 mi. N of Trinidad, US 101, T8N, R1W, S14, *Plett 30* (HSC); 3 mi. E of Bridgeville, *Roderick 60-220* (JEPS); S of Kneeland,

T3N, R3E, S19, 2,200 ft., *Rogers 29* (HSC); Redwood Creek, Garberville, *Shapovalov & Woodhull s.n.* (DS); 3 mi. E of Redwood Creek on old CA 299, *Spellenberg et al. 1361* (HSC); 1 mi. E of CA 299 on Lindsay Road, T6N, R1E, *Stevens 2* (HSC); 3 mi. SE of Korbel, Snow Camp Road, T6N, R2E, S34, *Styskel 6* (HSC); Van Duzen River, opposite Buck Mt., 1 mi. W of Dinsmores, 2,500 ft., *Tracy 18611* (UC, WTU); Hydesville, 200 ft., *Tracy 4017* (GH, NY, UC, US, WTU); 300 ft., *Tracy 5419* (UC); Glendale, Mad River, 0–500 ft., *Tracy 2156* (UC); Big Lagoon, 300 ft., *Tracy 10941* (UC); Dinsmores Ranch, Van Duzen River, opposite Buck Mt., 2,500 ft., *Tracy 4223* (UC, WTU); Lawrence Creek, Kneeland Prairie, 2,000 ft., *Tracy 6615* (UC); 20 mi. W of Pepperwood, US 101, 65 m, *Utech 88-025* (CM); Durphy Creek junction S Fork Eel River, US 101, 50 m, *Utech 88-019* (CM); Fisher Redwood Grove, 110 m, *Utech 88-027* (CM); 0.1 mi. N of Meyers Flat, S Fork Eel River, 60 m, *Utech 88-023* (CM); Cheatham Redwood Grove, 90 m, *Utech 88-026* (CM); Clark Redwood Grove, 40 m, *Utech 88-024* (CM); 1.5 mi. S of Miranda on US 101, 85 m, *Utech 88-022* (CM); S Fork Bear Creek, 2.5 mi. S of Shelter Cove, 1,840 ft., *White 16* (HSC). MARIN CO.: W end Alpine Lake, *Berg s.n.* (UC); Mill Valley, *Brandegee s.n.* (UC); Cascade Canyon, 0.75 mi. from Mill Valley Station, 350 ft., *Breedlove 2331* (DS); Lagunitas Creek, *Chestnut & Drew s.n.* (UC); Alpine Dam, *Covel s.n.* (CAS), *Doutt 137* (CM); Mt. Tamalpais, *Davy 795* (UC); Mill Valley, *Eastwood 2450* (CAS, GH, NY, UC, US); Sausalito, *Edwards s.n.* (NY); Phoenix Lake Road, 1 mi. below Lake Lagunitas, *Ewan 9424* (WTU); Mill Valley, *Grant s.n.* (GH, US); Mt. Tamalpais, *Greene s.n.* (CM, DS, MO, NY, UC, US, WTU); Sausalito, *James s.n.* (NY, US), *Kellogg s.n.* (JEPS), *Kellogg s.n.* (CAS), *Kellogg & Harford 984* (CAS, GH, NY, US), *LeRoy s.n.* (NY); Mill Valley, *Jepson s.n.* (JEPS, NY, US, WTU), *Jepson s.n.* (JEPS, NY), 100 ft., *Rose 34020* (WTU), *39008* (UC), *Zeile s.n.* (CAS); Mt. Tamalpais, Lagunitas Road, *Mason 1231* (GH, UC); Sequoia Canyon, *Michener & Bioletti 203* (GH, NY, UC); Kentfield, *Nelson s.n.* (ROPA), *Parsons s.n.* (CAS); Mt. Tamalpais, *Parks s.n.* (UC); 2 mi. SE of Nicasio on Lucas Valley Road, *Rentz 4* (CAS); Mt. Tamalpais, Pipeline trail, *Schreiber 112* (UC); Mt. Tamalpais, N end of Catarack trail, *Serpa 9* (ROPA); W side of Bolinas Ridge, E of Bolinas Lagoon, 750 ft., *Sharsmith 5174* (UC); W slope of Mt. Tamalpais, 1 mi. past Alpine Dam, 200 m, *Utech 88-016* (CM); W slope of Mt. Tamalpais, between Rock Springs and Alpine Dam, 430 m, *Utech 88-014* (CM); Nicasio Valley Road, San Geronimo to Nicasio, 90 m, *Utech 88-017* (CM); SW end of Alpine Lake, 320 m, *Utech 88-015* (CM); Tamalpais, T1N, R6W, 300 ft., *Yates 5039* (UC). MENDOCINO CO.: Ft. Bragg, *Arnold s.n.* (ROPA); Kaisen District, *McMurphy 182* (DS, NY); S Fork Big River, T17N, R17W, S29, 5 ft., *Seacat & Seymour 195* (HSC); Masonite Demonstration Forest off CA 128, 50 ft., *Smith & Wheeler 5143* (CAS); Hendy Woods State Park, *Smith & Wheeler 5136* (CAS); Faulkner County Park, 2.3 mi. W of Booneville, 290 m, *Utech 88-038* (CM); 2.7 mi. W of Comptche, 10 m, *Utech 88-036* (CM); 1.0 mi. W of Hollow Tree on CA 1, 350 m, *Utech 88-028* (CM); 1.7 mi. E of Flynn Creek Road on CA 128, 25 m, *Utech 88-037* (CM); 5.0 mi. past Rockport on CA 1 to Leggett, 5 m, *Utech 88-030* (CM); near Usal on CA 1, 80 m, *Utech 88-029* (CM); Dora Creek, Smith Redwood Grove, 140 m, *Utech 88-018* (CM); SSE of Albion, 4.7 mi. E on Navarro Ridge Road, 175 ft., *Utech et al. 84-069*
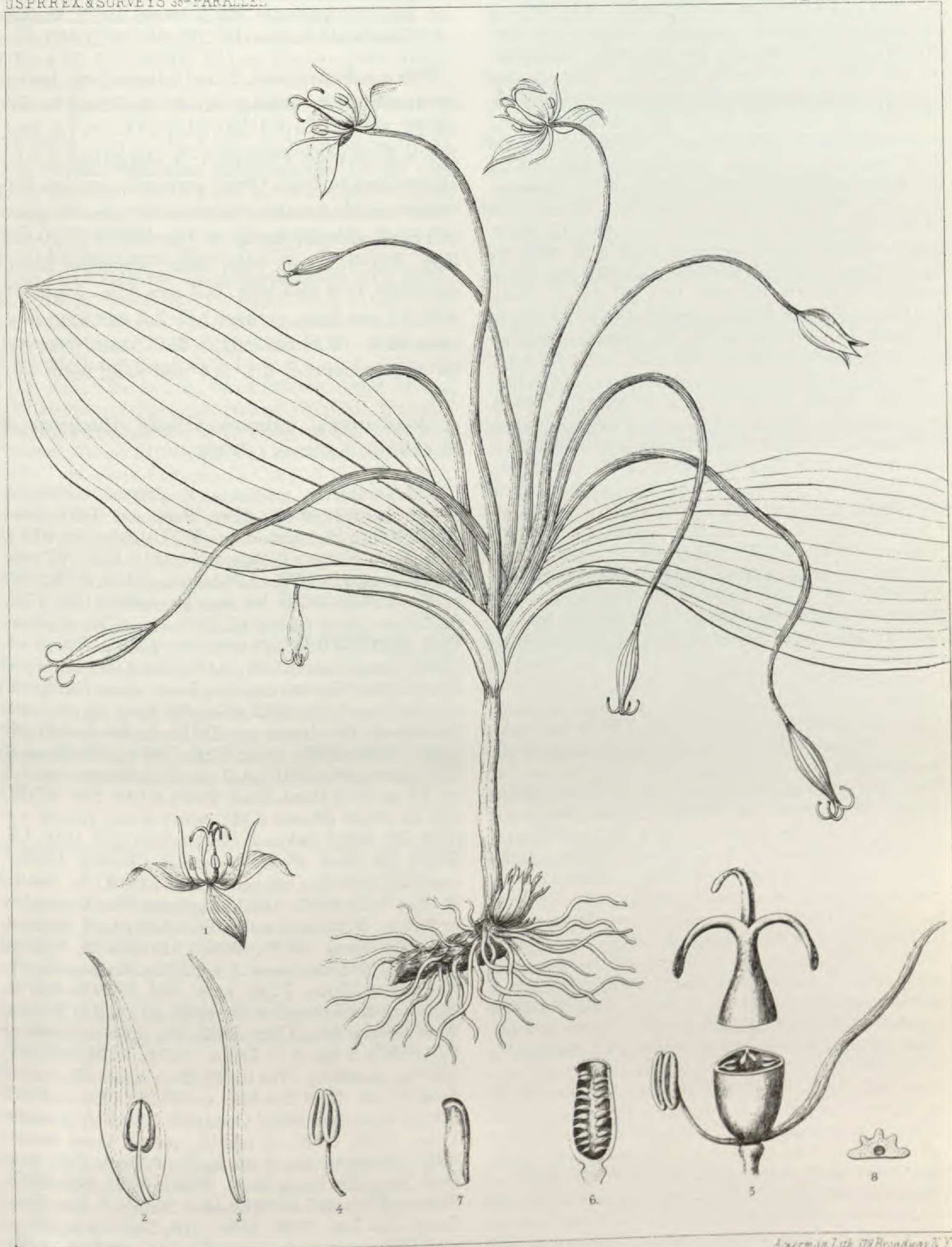
FIGURE 8. Type illustration of *Scoliopus bigelovii* from Torrey (1857).

(CM); SSE of Albion, 4.3 mi. E on Navarro Ridge Road, 220 m, *Utech et al. 84-056A* (CM); Jackson State Forest, N Fork of S Fork of Noyo River, 200 ft., *Wheeler 972* (CAS); Reeves Canyon Road, 3 mi. W of US 101, 1,100 ft., *Wheeler & Smith 2051* (CAS); Hendy Woods State Park, 150 ft., *Wheeler & Smith 780* (CAS); Haven's Neck, 4 mi. N of Gualala, 75 ft., *Wheeler & Smith 1187* (CAS); Hales Grove, NW of CA 208, 1,150 ft., *Wheeler*

& Smith 1142 (CAS); 10 mi. W of Laytonville to Branscom, Wiggins 11592 (DS, WTU); Albion, 3 ft., Wyrick 95 (HSC). SAN MATEO CO.: Kings Mt., Abrams 2283 (DS, GH, MO, NY, US), Atkinson s.n. (US), Baker 322 (CAS, DS, GH, MO, NY, UC, US), Block s.n. (CAS), Dudley s.n. (DS), Elmer 4113 (MO, NY, US), Elmer 4559 (CAS, DS, MO, NY, UC, US), Howell 265 (CAS); 2,000 ft., Rose 64000 (CAS, NY), Thomas 194 (DS), Wright 53 (US); Bear Gulch, Abrams s.n. (CM, DS, MO, WTU); Woodside, Applegate 737 (DS); Redwood City, Bolander s.n. (NY); McGarvey Gulch, Kings Mt., Browne s.n. (WTU); Summit Springs, Burnham s.n. (GH); La Honda Road to Skyline Drive, Demaree 8918 (CM, MO); La Honda Creek, Dudley s.n. (DS); Lake Pilarcitos, Eastwood s.n. (CAS, DS, GH, NY, UC), Ebright s.n. (UC), Pitelka s.n. (UC); Butomo Canyon, Eastwood s.n. (CAS); Woodside, Edwards s.n. (WTU), Leithold s.n. (DS); Portola, La Honda Road, Hoover 3897 (NY, UC, US); Searsville Lake, La Honda Road, 1,000 ft., Keck 1359 (DS, MO, OSC, WTU); N of La Honda, Kraeger s.n. (JEPS); below Kings Mt., McMurphy s.n. (DS); Pilarcitos Canyon, Oberlander 87 (DS); NW of Woodside, SE of Half Moon Bay, 0.2 mi. N of King Mt., Roderick 61-015 (JEPS); Fire Trail Road, 2.1 mi. W from Skyline Blvd., SE of Half Moon Bay, Roderick 61-019 (JEPS); San Mateo Creek, SE end Buriburi bridge, Rossbach 214 (UC); Hillsboro, Smith s.n. (GH, US), Smith s.n. (JEPS); Kings Mt., 0.5 mi. below Skyline Drive, 2,000 ft., Thomas 8539 (DS); 0.5–3.3 mi. on Kings Mt. Road from Skyline Drive to Woodside, 250–580 m, Utech 88-039, 88-040, 88-041 (CM). SANTA CRUZ CO.: Glenwod, Davis s.n. (CAS); Glenwood, Demaree 7356 (CM); Camon Camp, Waddell Creek, Dudley s.n. (DS); Aptos Creek, 2.5 mi. N of Capitola, 120 ft., Penalosa 1480A (CAS); Big Tree Grove, Sonne s.n. (UC); Bean Creek, 1 mi. SW of Glenwood, 900 ft., Thomas 3842 (DS); 3.5 mi. from mouth of San Lorenzo River, 300 ft., Thomas 2897 (UC); San Lorenzo River valley, 3.5 mi. N of Santa Cruz on CA 9, Thomas 1896A (DS). SONOMA CO.: Pocket Canyon, Baker s.n. (ROPA); Guerneville, Baker s.n. (UC); Redwood Canyon, 2.5 mi. S of Ft. Ross, 100 ft., Gould 562 (UC); Sturgeon's Mills, 3 mi. NW of Sebastopol, Hagg 3 (ROPA); W of Sebastopol, Heller & Brown 5128 (DS, MO, NY, US); 0.5 mi. N of Occidental on road to Camp Meeker, 150 ft., Lloyd 2044 (JEPS); Occidental, Lobenstein s.n. (UC); Duncan's Mill, Rattan s.n. (CAS); 6 mi. NW of Occidental along Willow Creek Road, Roderick 63-1020 (JEPS); E of Plantation, Gualala River, Roderick 60-135 (JEPS); Duncan's Mill, Rubtzoff 3297 (CAS); S of Guernevillle, Rubtzoff 1407 (CAS); 0.5–3.0 mi. S of Ft. Ross on CA 1, 50–100 m, Utech 88-011, 88-012 (CM); Stillwater Cove Park, 10 m, Utech 88-013 (CM); 2.75–6.0 mi. W on Willow Creek Road, Occidental to Bridgehaven, 60–130 m, Utech et al. 88-005, 88-006, 88-007 (CM); 0.3 mi. WNW of Camp Meeker on Bohemian Road, Dutch Bill Creek, 50 m, Utech et al. 88-004 (CM); WNW of Sebastapol, 0.2 mi. S of Occidental, Sturgeon's Mill, 80 m, Utech et al. 88-002 (CM); 0.1 mi. SE of East Avenue, Occidental to Camp Meeker, 140 m, Utech et al. 88-003, 88-182, 90-224 (CM).

2. Scoliopus hallii S. Watson, Proc. Amer. Acad. 14: 272. 1879. TYPE: U.S.A. Oregon: Cascade Mountains, 1871, Hall 518 (holotype, GH; isotypes, MO, NY, photos CM).

S. bigelovii Torrey forma minor Baker, J. Linn. Soc. Bot. 17: 492–493. 1879. TYPE: U.S.A. Oregon: Cascade Mountains, 1871, Hall 518 (GH, MO, NY).

Stems subterranean, 2.5–10.0 cm long. Leaves 2(–3), elliptic to oblong, basally sheathing to subsessile, rarely mottled with purple, 8–14 cm long, 2.5–4.8 cm wide. Pedicels 1–5, elongating to 6.0–10 cm long in fruit. Outer perianth segments lanceolate to oblanceolate, mottled with yellowish green and lined with purple, up to 9-nerved, 6.5–10 mm long, 2.0–3.3 mm wide; inner segments linear-spatulate, 6–9 mm long, 0.3 mm wide. Filaments 2.0–3.7 mm long, anthers 1.9–2.3 mm long. Capsules 16.0–18.5 mm long, 5.5–7.5 mm wide; stylar arms recurved, 2.1–2.4 mm long; seeds 10–14.

Illustrations. Abrams (1940), Hitchcock et al. (1969), Eastman (1990).

Representative specimens examined. OREGON: BENTON CO.: foot of Mt. Alsea, Barss s.n. (OSC), Cook 10554 (OSC), Fleischman s.n. (WTU), Stutz s.n. (OSC); 6 mi. W of Philomath, Steward 6031 (OSC); NE slope Mt. Alsea, 6.5 mi. SW of Philomath, T13S, R7W, 200 m, Utech 88-042 (CM); NE slope Mt. Alsea, T13S, R7W, S2, 240 m, Utech 88-043 (CM); N slope of Mary's Peak, Peck 10703 (WILLU). CLATSOP CO.: Astoria, Bowen s.n. (ORE); Onion Peak, T10W, R4N, S22, 3,064 ft., Chambers 3218 (OSC). COOS CO.: Coos River, above Fish Hatchery, Sheldon 11760 (ORE); Coquille River, Myrtle Point, Sweetsen & Henderson s.n. (ORE); 14 km E of Myrtle Point, T28S, R9W, S13 SWSE, 700 m, Sundberg & Christensen 430 (ORE); 1.0 mi. E of Remote and 1.0 mi. NE on Rock Creek Road, T29S, R10N, S36 SENW, 125 m, Utech 88-406 (CM). DOUGLAS CO.: Howell s.n. (CAS, DS, ORE); Oakland, Howell 3887 (NY, ORE, US, WTU); Elk Head, Woodson s.n. GH; Glendale, Henderson 12217 (ORE); Umpqua River, T25S, R7W, 500 ft., Detling 3935 (ORE, OSC); Sugarpine Mt., Lookinglass to Reston, Williams s.n. (ORE); 14 km E of Florence, Kentucky Creek, T19S, R9W, S15 NWSE, 550 m, Sundberg & Christensen 375 (ORE); Wagoner Creek, 13 km S of Elkton, T23S, R8W, S35 SWNW, 135 m, Sundberg & Christensen 387 (ORE); 8 km E of Remote, W of Kenyon Mt., T30S, R9W, S6, 660 m, Sundberg 915 (OSC); 8 km S of Elkton, T23S, R7W, S19 NE, 320 ft., Sundberg 769 (OSC); Bear Creek Recreation Area, 31 mi. W of Roseburg on OR 42, 200 m, Utech 88-407 (CM); summit of Camas Mt., 2 mi. E of Camas Valley, T29S, R8W, S3 NESW, 440 m, Utech 88-408 (CM). JOSEPHINE CO.: 3 mi. up New Fiddler Mt. Road from Josephine Creek Road, T38S, R9W, S23 SESE, 910 m, White 587A (ORE); Mud Springs, S Fork Silver Creek, Flat Top, T36S, R9W, S19, Stansell & Planets s.n. (OSC). LANE CO.: Cougar Bend, Coast Fork of Willamette River, Taylor 625 (WILLU); Indian Creek, Swishome, Henderson 16873 (ORE); Big Fall Creek, Henderson 18460 (ORE); Big Fall Creek, gravel pit, Henderson 18504 (ORE); Elk Creek, 1.7 mi. W of Noti, T17S, R6W, S30, 450 ft., Ireland 1796 (ORE); Elk Creek, Noti, T17S, R6W, 450 ft., Detling 5092 (ORE); Wendling, Georgia Pacific tree farm, Mason 10446 (ORE); Alderwood State Park, 15 mi. SW of Junction City, Mason

10412 (ORE); Gunshot Creek, Mabel, *Mason 10414* (ORE); Mt. Popocatepetl, T19S, R10W, S17 SESE, *Auler s.n.* (OSC); 13.7 km NE of Lowell, N Fork Fall Creek, T18S, R1E, S25 NENE, 317 m, *Christy 2404* (ORE); 11.7 mi. W of Lorane on Siuslaw River Road, T20S, R6W, S3 NESW, 200 m, *Utech 88-045* (CM); Whittaker Creek, 0.5 mi. SW of OR 62/US 126, T18S, R8W, S16 SWSE, 130 m, *Utech 88-046, Utech 88-450* (CM); Doris wayside, McKenzie River and OR 15/US 126, T16S, R3E, S31 NESW, 250 m, *Utech 88-047* (CM); Shotgun Creek, 0.6 mi. SW of Marcola Road, T15S, R1W, S32 NWSW, 260 m, *Utech 88-048, Utech 88-463* (CM); Fall Creek, *Wynd 45* (UC). LINCOLN CO.: Van Duzen Forest along OR 18 and Salmon River, T6S, R9W, S20, 100 m, *Utech 88-051, Utech 88-527* (CM). LINN CO.: Lebanon, *Haskin 110* (ORE); Lacomb, 1.5 mi. E of Hammond Camp, T12S, R1E, S22 SESE, *Willis s.n.* (OSC); McDowell Creek Falls Park, 8.6 mi. E of US 20, T12S, R1E, S36, 270 m, *Utech 88-044, Utech 88-497* (CM). MARION CO.: Silverton, *Howell 577* (CM); Silverton, *Howell s.n.* (CAS, ORE, OSC); along stream, 1 mi. E of Silverton, *Nelson 2124* (GH). POLK CO.: along Luckiamute River, 1 mi. above Fisherman's Camp, T9S, R7W, S34, *Steward 6695* (OSC); Dutch Creek, ca. 2.5 mi. NNW of Falls City, T8S, R6W, S17 NESW, 220 m, *Utech 88-049* (CM); Little Luckiamute River, 2.0 mi. NW of Falls City, T8S, R7W, S23 SENE, 320 m, *Utech 88-050* (CM); Van Duzen Forest along OR 18 and Salmon River, T6S, R8W, S10, 100 m, *Utech 88-053* (CM). TILLAMOOK CO.: bank of Wilson River, 15 mi. from Tillamook, *Thompson 4117* (CAS, CM, MO, NY, ORE, US, WTU); Van Duzen Forest along OR 18 and Salmon River, T6S, R9W, S17, 110 m, *Utech 88-052* (CM); Trask River, 10 mi. E of Tillamook, 120 m, *Utech 88-054* (CM); Wilson River at Keenig Creek, 18 mi. NE of Tillamook, T1N, R8W, S25, 120 m, *Utech 88-055* (CM); Munson Creek Falls County Park, 100 m, *Utech 88-540* (CM).

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